Integration of a fish bioenergetics model into a spatially explicit water quality model: Application to menhaden in Chesapeake Bay

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ABSTRACT

Although fish are usually thought of as victims of water quality degradation, it has been proposed that some planktivorous species may improve water quality through consumption of algae and sequestering of nutrients via growth. Within most numerical water quality models, the highest trophic level modeled explicitly is zooplankton, prohibiting an investigation of the effect a fish species may be having on its environment. Conversely, numerical models of fish consumption do not typically include feedback mechanisms to capture the effects of fish on primary production and nutrient recycling. In the present study, a fish bioenergetics model is incorporated into CE-QUAL-ICM, a spatially explicit eutrophication model. In addition to fish consumption of algae, zooplankton, and detritus, fish biomass accumulation and nutrient recycling to the water column are explicitly accounted for. These developments advance prior modeling efforts of the impact of fish on water quality, many of which are based on integrated estimates over an entire system and which omit the feedback the fish have through nutrient recycling and excretion. To validate the developments, a pilot application was undertaken for Atlantic menhaden (*Brevoortia tyrannus*) in Chesapeake Bay. The model indicates menhaden may reduce the algal biomass while simultaneously increasing primary productivity.

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1. Introduction

As early as the 1960s–70s intense eutrophication events have occurred in sensitive estuaries, with increasing anthropogenic sources of nitrogen (N) and phosphorus (P) leading to excessive algal growth, degradation of water quality, and a general decline in ecological health (Cloern et al., 2007). If not consumed by planktivores, algal biomass dies and sinks to the sea floor, where oxygen consumption during the decay leads to anoxic regions and the destruction of benthic habitat (Jonas and Tuttle, 1990). Although eutrophication is traditionally controlled with nutrient load reduction, difficulty in implementation has led to consideration of more innovative techniques. One proposed strategy is revitalizing planktivorous fish, which remove algae from the water column as they filter feed and sequester nutrients during growth. In order to make informed decisions on the viability of this eutrophication management technique, a method is needed to quantify the potential effects of fish populations on water quality.

One option is extending eutrophication models, used previously to determine the impacts of various nutrient sources (and the presence of benthic filter feeders such as oysters) on estuarine systems such as Chesapeake Bay (Cerco and Noel, 2005, 2007; Cerco, 1995a,b). In the present formulation, a fish bioenergetics model (FBM) of fish consumption, growth, and nutrient recycling is incorporated into the eutrophication model CE-QUAL-ICM. The new model system is applied to investigate the effect changes in the population of Atlantic menhaden (*Brevoortia tyrannus*), a planktivorous fish species, might have on the water quality in Chesapeake Bay.

Chesapeake Bay (Fig. 1) is the largest estuarine system in the United States, spanning approximately 320 km in length, 55 km wide at its widest point, and holding about 57×10^9 cubic meters of water. It supports more than 3600 species of aquatic animals and 2700 plant species, and over 16 million people live and work throughout the watershed (Chesapeake Bay Program, 2009). The system suffers from anthropogenic eutrophication characterized by high nutrient concentrations, diminished water clarity, and bottom-water anoxia (Kemp et al., 2005). One strategy proposed for managing eutrophication in Chesapeake Bay is increasing the numbers of Atlantic menhaden found in the estuary and thereby reducing algal biomass and associated deleterious effects. Estuarine systems serve as nursery grounds for this species as they progress from young larvae, who feed by individual acts of capture on zooplankton, to filter-feeding juveniles and adults (Rogers and Van Den Avyle, 1989). Adults may also be found in estuarine waters during the spring and summer.

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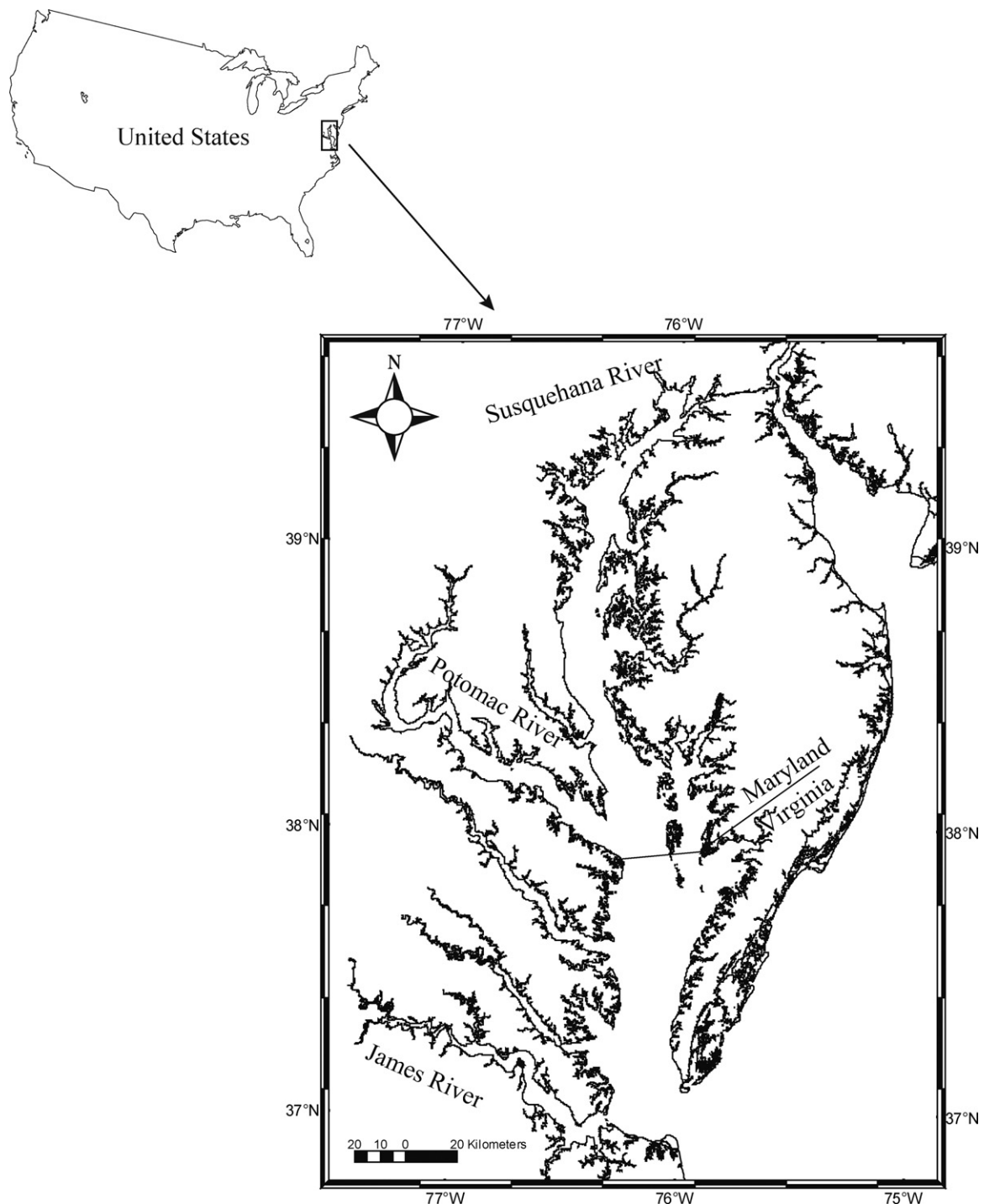 *E-mail address:* Patricia.A.Dalyander@usace.army.mil (P.S. Dalyander).

Fig. 1. Map depicting the location of Chesapeake Bay.

Some efforts have been made to quantify the effects of planktivorous fish on water quality in Chesapeake Bay. Boynton et al. (1995) examined various sources and sinks of nutrients in the system and determined grazing on phytoplankton by planktivorous fish is great enough that changes in their population can impact the nutrient levels in the bay. Other studies have estimated the amount of phytoplankton menhaden consume through the use of bioenergetics models of fish growth. Rippetoe (1993) developed a model for age-0 menhaden in Chesapeake Bay; although he concluded that only 3–5% of the total primary production could be consumed by juvenile menhaden, older fish were not included within the study, and the author noted that the ability of menhaden to consume iso-

lated patches of phytoplankton may enhance their effects. Gottlieb (1998a,b) evaluated the impacts of fishery management for age-0 and age-1 to age-3 fish and concluded that age-0 fish could remove 1.5–119% of the primary productivity, whereas older fish could consume ~10–60% of the primary production. These models are limited, however, in that they neglect feedback to the water column, consider primary productivity rather than algal biomass (the more fundamental problem), and are spatially averaged. Menhaden may have a more significant impact on the total algal biomass over time by consuming highly concentrated patches of algae than the equivalent biomass spread out in sparsely concentrated patches, an effect which is lost in a spatially averaged approach where
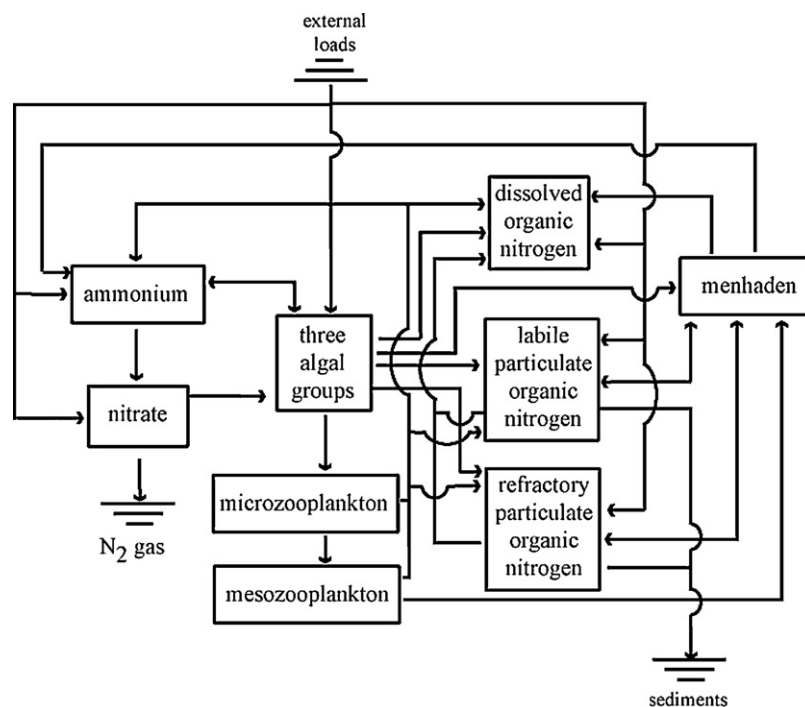
Fig. 2. Conceptual model of the nitrogen cycle in CE-QUAL-ICM.

only the total quantity of biomass consumed is considered. The current study improves the state-of-the-art in eutrophication modeling by coupling a fish bioenergetics model into a high-fidelity water quality model, and allows for an investigation of the order-of-magnitude impact menhaden have or could have on Chesapeake Bay.

2. Model formulation

The basis for the coupled models is the eutrophication model CE-QUAL-ICM, to which schools of fish have been explicitly added. Fish movement is based on replicating observed seasonal distribution of menhaden in Chesapeake Bay; food consumption, biological processes, and nutrient recycling to the water column are dictated by a fish bioenergetics model. The details of the eutrophication model, fish movement, and the FBM are outlined below.

2.1. Eutrophication model

CE-QUAL-ICM is a three-dimensional eutrophication model that has seen extensive application as part of the Chesapeake Bay Environmental Model Package (Cerco and Cole, 1993; Cerco and Noel, 2005, 2007, 2004, 2001; Cerco et al., 2004; Cerco, 1995a,b) and elsewhere (Cerco et al., 2003, 2006; Cerco and Seitzinger, 1997). Within Chesapeake Bay, the model has been implemented on grids of various size and resolution; a grid with 4073 cells was used in this study. The volume of the grid cells varies from 1.5 to 160×10^6 m^3, with an average volume of 25×10^6 m^3. The model time step is determined by numerical stability criteria and is, on average, 10–15 min. CE-QUAL-ICM relies on an external hydrodynamics model, in this case CH3D-WES, with the details of formulation found elsewhere (Johnson et al., 1993). CE-QUAL-ICM operates on a set of state variables belonging to categories including physical variables (salinity, temperature, etc.) and elemental cycles, e.g., carbon, nitrogen, phosphorus, silica, and oxygen (Cerco and Noel, 2005; Cerco and Cole, 1993). In the current formulation, active constituents are temperature, salinity, inorganic suspended solids, three algal groups

(nominally representing blue-green algae, spring diatoms, and green algae), two zooplankton groups (representing micro- and mesozooplankton), ammonium, oxidized nitrogen (nitrite/nitrate), dissolved oxygen, and various labile and refractory forms of dissolved and particulate carbon, nitrogen, phosphorus, and silica. In each elemental cycle, mass is conserved. In the nitrogen cycle, for example, nitrogen in ammonium and nitrate is utilized by algae, which subsequently may die and return the nitrogen to the water column in the form of particulate or dissolved organic nitrogen or ammonium, or be consumed by an explicitly modeled predator (Fig. 2). The full details of the CE-QUAL-ICM model formulation and descriptions of application to Chesapeake Bay may be found elsewhere (Cerco and Cole, 1993; Cerco and Noel, 2005, 2004).

2.2. Menhaden dynamics

Menhaden are added to the model as "schools", noting that all members of a school are identical. School movement, population size and structure, and other characteristics are based on observations, thus distinguishing the FBM model in this application from "Individual-Based Models" (IBMs) or "Agent-Based Models" (ABMS) wherein both behavior and growth of discrete individuals are determined in response to their environment (Grimm and Railsback, 2005). Schools are segregated by age class, with schools consisting of either (1) entirely age-0 fish, (2) a mix of age-1 and age-2 fish, or (3) entirely age-3 fish (McHugh et al., 1959). Although the life expectancy for menhaden can be 10–11 years, truncation of the population has resulted in a dramatic reduction in the number of older fish (Gottlieb, 1998b); fish older than age-3 contribute negligibly to the population and are excluded from the model. The initial population size for each school was randomly selected from a Gaussian weighted distribution around a mean value of 4.4×10^5 members, an approximate size of menhaden schools as determined from both aerial LIDAR (Light Detection and Ranging) estimates and purse seine haul data (A. Sharov, personal communication, April 3, 2009).

Table 1
Description of the parametric cases of menhaden population and fishing pressure considered.

	Age-0		Age-1			Age-2			Age-3		
Test case	N_0	AFM	APM	N_0	AFM	APM	N_0	AFM	APM	N_0	AFM	APM
Baseline ($\times 10^9$)	1.37	0.02	1.23	0.42	0.22	0.72	0.18	0.85	0.60	0.05	1.37	0.55
Low population			Half initial population, same fishing mortality									
High population			Double initial population, same fishing mortality									
"Historic" population			$5\times$ initial population, zero fishing mortality									
High fish. mortality			Same initial population, double fishing mortality									
Low fish. mortality			Same initial population, half fishing mortality									
Zero fish population			Zero population									

N_0 = Population entering the grid (billions of fish).
AFM = Instantaneous annual fishing mortality (year^{-1}).
APM = Instantaneous annual natural (predation) mortality (year^{-1}).
Baseline population: 10% of estimated average total Atlantic menhaden stock, 1985–2005[1].
Baseline mortality: average of fishing mortality-by-age, 1985–2005; stock assessment natural mortality[1].
[1] Atlantic States Marine Fisheries Commission, 2006.

Interannual variability combined with a lack of data makes fixing the total number of menhaden entering Chesapeake Bay during winter and spring difficult. Values for the baseline case were taken by assuming 10% of the total Atlantic stock enters Chesapeake Bay during a season, with the total Atlantic stock taken as the average of the estimated population for 1985–2005 (Atlantic Menhaden Technical Committee, 2006). The biomass of menhaden in Chesapeake Bay compared to the total Atlantic menhaden stock has been estimated at approximately 20% of the unfished stock for 1999–2000 (Uphoff, Jr., 2003a), indicating a 10% estimate may be conservative. The Chesapeake Bay population values are within the same order of magnitude as initial population estimates ($1.5–18.5 \times 10^9$ age-0 fish, 3×10^9 age-1 fish, 2.45×10^9 age-2 fish, and 0.28×10^9 age-3 fish) made by back-calculating population from estimates of fishing mortality, total haul by the fishery, and distribution of the catch between age classes, and validated against other estimates of population within the literature (Gottlieb, 1998b). Runs with a population of twice and half the baseline population were conducted to determine sensitivity to this parameter; two 'extreme' cases were also considered. A zero menhaden population case provides an estimate of the effect the baseline population is having. A five times baseline (with zero fishing mortality) gives an order of magnitude estimate of the potential impacts of a population closer to historic levels, although historically menhaden would have had a wider range and varying distribution of age classes (McHugh et al., 1959). Given the total Atlantic menhaden population went from 15 to 25×10^9 members in the 1950s (with fishing) to approximately 3.7×10^9 members by 1998 (Uphoff, Jr., 2003b), the five times baseline estimate may be conservative for historic numbers.

Within the model, the population of each school decreases as a result of mortality:

$$\Delta N = \Delta N_{stv} + \Delta N_{suf} + \Delta N_{prd} + \Delta N_{fsh}$$

The total number of individuals lost (ΔN) within a time step (Δt) is the sum of the number lost due to starvation (ΔN_{stv}) and suffocation (ΔN_{suf}), accounted for explicitly as functions of fish condition and model environment, along with the number lost to other natural causes (ΔN_{prd}, primarily predation in the case of menhaden) and those caught by the fishery (ΔN_{fsh}). The number lost due to any specific process is a function of the mortality rate for that process, e.g., for starvation:

$$\Delta N_{stv} = N_t \cdot M_{stv} \cdot \Delta t$$

M is mortality (fish/s) and N_t is the school's population. Starvation and suffocation were accounted for based on models developed for Chesapeake Bay anchovy (Adamack, 2007). If the wet weight drops below 70% of the 'healthy' weight for that length, a daily mortality rate of 0.1 fish/day is introduced to the school (converted to instan-

taneous mortality rate in fish/s as $M_{stv} = DFST/(24 \cdot 60 \cdot 60)$, where DFST is the daily mortality rate). 'Healthy' weight is calculated from an empirically determined length/weight relation (Rippetoe, 1993):

$$WW_{ind,healthy} = 7.1e - 6 \cdot L^{3.07}$$

WW is the wet weight (g) and L is the length (in mm). Suffocation mortality is calculated as (Adamack, 2007):

$$DFSU = 0.093487 + 70.11894 \cdot (\ln[DO_{cell}])^2 \quad \text{if} [DO_{cell}] \leq 1 \, \text{mg/l}$$
$$= 0 \, \text{if} [DO_{cell}] > 1 \, \text{mg/l}$$

$[DO_{cell}]$ is the concentration of dissolved oxygen (mg/l). Predation and fishing mortality are calculated from values reported in the literature (Table 1) for the entire Atlantic menhaden stock. Given that an estimated 52% of the total fishing haul comes from Chesapeake Bay (Smith, 1999), and the baseline population is taken as 10% of the Atlantic stock, fishing mortality is likely underestimated, but no data exist to robustly estimate mortality rates for the Bay specifically. For comparison, the model was also run with twice, half, and no fishing mortality (Table 1). Fishing mortality is spatially and temporally uniform throughout a model run. Realistically, fishing pressure varies throughout the season, and there is a strong spatial variance as a result of purse seine fishing being prohibited in Maryland waters but allowed by Virginia; however, insufficient data exist to accurately model this variation.

School movement is controlled via a biased Monte Carlo simulation parameterized to replicate the observed distribution of menhaden in Chesapeake Bay (e.g., schools do not respond to environmental cues). Schools of menhaden enter the mouth of the model grid between January 1 and March 31, with a mean entry date of February 15 and a standard deviation of 20 days, replicating their entrance into Chesapeake Bay in the winter and early spring (Fabrizio and Montane, 2007; Longstaff et al., 2008). School location is updated every six hours, with the migration velocity randomly selected from a Gaussian distribution with a mean of 10 km/day and a standard deviation of 5 km/day, and forced to be between 0 and 15 km/day, reasonable compared to Atlantic menhaden swimming speed (Durbin et al., 1981). Swimming direction for model dates prior to March 11 is selected from a Gaussian distribution parameterized to force the schools to come up the stem of the bay toward the head, while the same process is used in reverse after October 17 to bring the schools back out of the bay. During the rest of the year, fish direction is unbiased. The migration model has been empirically calibrated to distribute the schools throughout the main stem of the bay and modeled rivers where menhaden have been observed in the field (Love et al., 2006; Bonzek et al., 1991). Depth is randomly

selected from a Gaussian distribution with a mean of 1.5 m and a standard deviation of 0.75 m.

Although a more detailed method to parameterize movement would be preferred, data on menhaden spatial distribution in Chesapeake Bay are limited. While there have been attempts to track the schools with LIDAR (Longstaff et al., 2008), insufficient data exist for calibrating the model. Other available data rely on reports from fishery logs, which do not represent a detailed systemic survey. Studies have found correlation between lower salinity in estuaries and relative abundance of young menhaden (Rogers and Van Den Avyle, 1989) and an association of the distribution of juvenile menhaden with changes in chlorophyll concentration and other environmental factors (Friedland et al., 1996; Friedland and Haas, 1988); in addition, menhaden in Chesapeake Bay are distributed somewhat by length (a function of age class as well as variation between individuals), with smaller fish congregating in fresher water up the river mouths and older fish found more in the main stem (McHugh et al., 1959). This information, however, lacks sufficient temporal and spatial resolution for detailed model calibration. Fish distribution was parameterized to match the observed seasonally variant patterns, and was fixed between model runs to isolate the effects of population changes.

2.3. Fish bioenergetics model

Bioenergetics models rely on conservation principles, with the amount of energy a fish devotes to growth being the difference between that which is obtained via consumption and that which is lost through life-process expenditures. The present formulation is based on the Wisconsin Fish Model (Hanson et al., 1997). The rate of wet weight growth is calculated as:

$$\frac{\partial WW}{\partial t} = \{C' - [(R' + S') + (F' + U')]\} \cdot \frac{1}{E_{pred}}$$

$\partial WW/\partial t$ is the rate of wet weight growth (g/s); E_{pred} is the energy density of the fish (J/g). Other variables are the rates of energy uptake of consumption (C'), respiration (R'), specific dynamic action (S'), egestion (F'), and excretion (U'). Fish energy density at time 't' is calculated as a linear function of representative individual weight:

$$E_{pred,t} = PRDA \cdot WW_{ind,t}$$

PRDA is an empirically determined predator energy density and is taken as 8717.3 J/g for age-1 and up fish (Durbin and Durbin, 1998) and 3937.6 J/g for age-0 fish (Rippetoe, 1993).

Energy consumption (C') is a function of the volumetric clearing rate of the fish and the available food energy within a computational grid cell. A feeding fraction (empirically determined as 0.75) is introduced to avoid unrealistically large growth in modeled fish, which feed at all times, compared to biological fish, which consume food only during a portion of their waking hours.

The three types of prey considered within the model are phytoplankton, mesozooplankton, and detritus. The total algal concentration is the sum of the three model algae species. Although the model contains both micro- and mesozooplankton, low retention efficiency for microzooplankton precludes them as a source of food for menhaden. Detrital food sources can be significant for menhaden (Deegan et al., 1990; Lewis and Peters, 1984). Detritus in the eutrophication model is comprised of elemental forms (carbon, nitrogen, phosphorus, silica) of particulate matter, the sum of which is taken as the dry detritus weight.

The volumetric clearing rate for Chesapeake Bay menhaden is based on fish physiology which, in turn, depends on length (L), and water temperature (T) (Luo et al., 2001):

$$V'_s = f(DO) \cdot gap(L) \cdot u(T, L) \cdot eff(L)$$

V'_s is the volumetric clearing rate (m³/s) and is based on the mouth gap area (gap, in m²), swimming speed (u, in m/s), an empirically derived function of dissolved oxygen concentration within the cell the school occupies ($f(DO)$), and filtration efficiency (eff(L), unitless). The dependence on dissolved oxygen is based on physiological fish response to stress (Luo et al., 2001):

$$f(DO) = \frac{1}{1 + \exp(-2.1972 \cdot [DO] + 6.5916)}$$

[DO] is the concentration of dissolved oxygen. The mouth gap area is a function of body length (Luo et al., 2001):

$$gap(L) = 0.2586e - 5 \cdot (L)^{1.79767}$$

Swimming speed in menhaden is a function of body length and food concentration, with fish exhibiting one characteristic swimming rate (in body lengths/s) when chlorophyll concentration exceeds a threshold to trigger 'feeding' behavior and a second, slower rate when chlorophyll does not exceed this threshold (Durbin and Durbin, 1975; Durbin et al., 1981). Therefore, swimming velocity is calculated as:

$$u = 1.67 \cdot \frac{L}{1000} \quad \text{if Con}_{CHL} > 0.004 \, \text{mg/l}$$

$$= 0.47 \cdot \frac{L}{1000} \quad \text{if Con}_{CHL} < 0.004 \, \text{mg/l}$$

Con_{CHL} is the concentration of chlorophyll (g/m³).

Filtration retention efficiency is based on fitting a sigmoid response curve to known values (20% at 50 mm, 50% at 200 mm) (Luo et al., 2001):

$$eff(L) = 0.5/(1 + \exp(-0.0527811 \cdot L + 2.96973))$$

In reality, retention for all age classes is dependent on prey size, and the gill raker spacing of adults may prohibit retention of smaller prey species (Ahrenholz, 1991; Friedland et al., 2006). The water quality model does not contain size data for prey; therefore, this dependence was not captured. Although menhaden larvae consume zooplankton by individual acts of capture, Atlantic menhaden transition to the filter-feeding juvenile stage at between 30 and 40 mm in length, smaller than their entry size of 48 mm (Ahrenholz, 1991). In addition to prey size constraints, some algae of certain types are capable of passing through a fish gut in a viable form, including blue-green algae through Atlantic menhaden (Friedland et al., 2005), and adults and juveniles may have different algal consumption rates (Lynch et al., 2010); however, species and age dependent retention was not included in the present formulation.

Combining phytoplankton, zooplankton, and detrital food sources, and accounting for filtration efficiency (eff, unitless), the total rate of energy consumption becomes:

$$C' = F_{Frc} \cdot \left(\frac{Con_{phyto}}{CtWP} \cdot EPLK + \frac{LZ}{CtWZ} \cdot EZOO \right.$$
$$\left. + \frac{Con_{det}}{DWWW_{det}} \cdot EDET \right) \cdot V'_s$$

F_{Frc} is the feeding fraction (unitless). Con_{phyto} is the concentration of algae in model units of grams of carbon/m³, converted with a carbon to wet weight ratio (CtWP, in gC/gWW) taken as 0.1 (Peters and Downing, 1984) to wet weight concentration and multiplied by the energy density for phytoplankton taken as 6020 J/g (Rippetoe, 1993). Similarly for zooplankton (model concentration "LZ" in gC/m³), CtWZ = 0.04344, based on a gDW/gWW ratio of 0.1086 (Durbin and Durbin, 1998) and a gC/gDW ratio of 0.4, and multiplied by the energy density of zooplankton taken as 2790 J/g (Rippetoe, 1993). The total dry concentration of detritus (Con_DET) was converted to wet weight assuming a dry weight to

Table 2
Fish bioenergetics model input parameters.

Parameter	Fish age class			
	Age-0	Age-1	Age-2	Age-3
Entry characteristics				
Entry weight	1 g[a]	85.6 g[b]	167.1 g[b]	284.8 g[b]
Entry length	48 mm[c]	202 mm[c]	252 mm[c]	300 mm[c]
Bioenergetics				
RESA	0.003301[a]	0.00294[b]	0.0027[b]	0.003[b]
RESB	−0.2246[a]	−0.0085[b]	−0.01[b]	−0.01[b]
RTO	33 °C[a]	33 °C[b]	33 °C[b]	33 °C[b]
RTM	36 °C[a]	36 °C[b]	36 °C[b]	36 °C[b]
QR	2.07[a]	2.5[b]	2.5[b]	2.5[b]
SDA	0.1[a]	0.1[b]	0.1[b]	0.1[b]
FA	0.14[a]	0.14[b]	0.14[b]	0.14[b]
UA	0.10[a]	0.10[b]	0.10[b]	0.10[b]

[a] Rippetoe (1993).
[b] Gottlieb (1998b).
[c] Based on initial weight and weight/length relationship for menhaden.

wet weight ratio of 0.2 and multiplied by a fixed energy density of 900 J/g (Rippetoe, 1993). Although actual detrital energy density has a complex dependence on composition not captured with the model constituents (Tenore, 1981), the relatively low energy value of detritus compared to phytoplankton and zooplankton (found in abundance in Chesapeake Bay during menhaden residency) will make the resultant error in fish growth small, since even at similar mass consumption rates for detritus the growth will primarily be a result of the energy consumed from those higher value food sources. Including detritus consumption does, however, allow modeling transformation of carbon, nitrogen, and phosphorus between model constituents due to consumption by menhaden.

Energy is lost due to physiological processes including respiration, specific dynamic action, excretion, and egestion. Rate of energy loss to respiration is determined from mass consumption of oxygen. R'_O is calculated from physiological parameters specific for menhaden (RESA, RESB), a temperature dependence function, and an activity multiplier.

$$R' = R'_O \cdot E_O$$

$$R'_O = \text{RESA} \cdot \text{WW}_t^{\text{RESB}} \cdot f(T) \cdot \text{ACT} \cdot (WW_t/86400)$$

R'_O is the rate of oxygen consumption (g/s); E_O is an oxycalorific coefficient (J/g O_2); RESA and RESB are physiological parameters (see Table 2); $f(T)$ is a temperature dependency function, and ACT is an activity multiplier. The temperature dependence of oxygen consumption is calculated as (Hanson et al., 1997):

$$f(T) = V^X \cdot \exp(X \cdot (1 - V))$$
$$V = (\text{RTM} - T)/(\text{RTM} - \text{RTO})$$
$$X = (Z^2 \cdot (1 + (1 + 40/Y)^{0.5})^2)/400$$
$$Z = \text{LN}(RQ) \cdot (\text{RTM} - \text{RTO})$$
$$Y = \text{LN}(RQ) \cdot (\text{RTM} - \text{RTO} + 2)$$

T is temperature (°C) and RQ, RTM, and RTO are menhaden-specific parameters (Table 2). Since swimming velocity in the model is dependent on chlorophyll-triggered feeding state, a similar behavior dependence is introduced into the activity multiplier and the oxycalorific coefficient is based on empirical observation of Atlantic menhaden, with $E_{O,feed} = 13388.8$ J/g O_2; $E_{O,nonfeed} = 13723.5$ J/g O_2 (Durbin and Durbin, 1983). Because routine respiration rates were used to calibrate the bioenergetics respiration parameters used in this study, the activity multiplier during non-feeding times was taken as unity, $\text{ACT}_{nonfeed} = 1.0$ (Rippetoe, 1993); respiration rate among foraging menhaden has been observed to increase 2.2–5.4 times over routine respiration (Durbin and Durbin, 1983), there-

fore the activity multiplier during feeding times was taken as $\text{ACT}_{feed} = 3.5$.

The bioenergetics model assumes unlimited oxygen availability, which may not be true. If oxygen is limiting, the volumetric clearing rate previously calculated is used to determine the actual rate of oxygen mass consumption:

$$R'_O = V'_{s,max} \cdot [\text{DO}]$$

Egestion energy loss rate is calculated as a percentage of consumption, and excretion and specific dynamic action losses are calculated as a percentage of rate of energy assimilated (e.g., consumption minus egestion).

$$S' = \text{SDA} \cdot (C' - F')$$
$$F' = \text{FA} \cdot C'$$
$$U' = \text{UA} \cdot (C' - F')$$

2.4. Choice of bioenergetics parameters

FBMs are typically calibrated for a specific species through physiological testing in a controlled tank environment. The age-0 bioenergetic parameters (Table 2) are based on laboratory values determined via such testing using multiple food sources by Rippetoe (1993). In contrast, research into adult menhaden physiology has not focused on determining the allometric function parameters required by this bioenergetics model, and the difference in physiology between fish of different age classes may introduce error in the FBM if the same parameterizations are used. The parameter values used in the present study (Table 2) were attained by Gottlieb (1998b) by calibration to observed menhaden size over the course of the season in Chesapeake Bay. Observed sizes were fit to an exponential growth curve, and the fish bioenergetics parameters were selected to minimize the average squared error between the observed growth curve for each age cohort and an exponential fit to model fish growth (the Rippetoe physiological parameterizations for juvenile fish were used as a starting point).

2.5. Fish composition

In addition to energy, mass must be conserved. Mass assimilation by fish is a complex process (Rippetoe, 1993; Durbin et al., 1983) that changes in response to environmental stress, life stage, and other factors that are beyond the scope of this study (Deegan, 1986). In the model, idealized fish elemental composition was based on physiological measurements (Table 2). Elasticity is allowed wherein an elemental deficit can occur, with higher fractions of that element retained at future time steps to regain the target composition. The amount of a given element a fish needs to retain at each time step is calculated as:

$$\text{Need}_E = \text{WW}_{t+\Delta t} \cdot \text{DWWW} \cdot \text{TFEDW} - \text{WW}_t \cdot \text{DWWW} \cdot \text{FEDW}_t$$

This amount (Need_E) is a function of the dry weight to wet weight ratio (DWWW, unitless), the wet weight before and after the time step (WW, g), the target fraction of that element (TFEDW, unitless), and the actual fraction of that element at the previous time step (FEDW_t, unitless). The dry weight to wet weight ratio for age-0 fish is taken as 0.216 (Rippetoe, 1993), and for age-1+ as 0.334 (Durbin et al., 1983). The target fractions for carbon and nitrogen as a function of dry weight (TFCDW, TFNDW) were taken from values in the literature for Atlantic menhaden as 0.5661 and 0.0803, respectively (Durbin et al., 1983); the value for phosphorus as a function of dry weight (TFPDW) could not be found for Atlantic menhaden and a value for a closely related species, Gulf menhaden, was used instead, 0.024 (Deegan, 1993).

2.6. Fish interactions with the water quality model

To conserve mass on the model grid, prey constituent concentrations must decrease when consumed and fish outputs must return to the water column. For each algal group, B_k, a school's consumption rate is calculated from the volumetric clearing rate, the school's population, and the original concentration:

$$\frac{\partial B_k}{\partial t} = -V'_s \cdot N_{t+\Delta t} \cdot B_k$$

A similar calculation is performed for mesozooplankton. For other constituents, fish can either be producers (e.g., ammonium) or both consumers and producers (e.g., particulate matter). For each element considered within the model, a recycling rate is calculated as the total rate at which the element is returned to the water column by the fish.

Carbon mass balance dictates the growth rate in carbon units:

$$G'_C = C'_C - (R'_C + F'_C + U'_C)$$

G'_C is the growth rate in carbon (gC/s) and is a function of carbon uptake (C'_C, in gC/s), respiration (R'_C, in gC/s), egestion (F'_C, in gC/s), and excretion rates (U'_C, in gC/s). Carbon uptake is governed by fish consumption of algae, mesozooplankton (LZ) and labile and refractory particulate organic carbon (LPOC, RPOC):

$$C'_c = V'_s \cdot N_{t+\Delta t} \cdot \left(\sum_{k=1}^{3} B_k + LZ + LPOC + RPOC \right)$$

Inorganic carbon is not explicitly accounted for in the model; however, the loss of carbon due to respiration must be considered. The rate of carbon emission due to respiration is:

$$R'_c = \frac{R'_O}{AOCR}$$

R'_c is the rate of carbon emission (gC/s) and is a function of the rate of oxygen consumption and the oxygen-to-carbon ratio in respiration (AOCR, in gO_2/gC). Using a simple model for aerobic respiration:

$$C_6H_{12}O_6 + 6O_2 \rightarrow 6CO_2 + 6H_2O$$
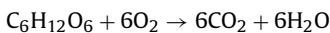
6 moles of dissolved oxygen respired produce 6 moles of carbon dioxide, which converts to an AOCR of 2.67 g O_2 g^{-1} C.

The ideal carbon recycling rate (CRRATEf, in gC/s/fish) is therefore:

$$CRRATEf = F'_C + U'_C = C'_C - G'_C - R'_C = C'_C - Need_C - \left(\frac{R'_O}{AOCR} \right)$$

If the calculated recycling rate were to fall below zero, the fish would (unrealistically) absorb carbon from the water column, therefore, the actual carbon recycling rate is calculated as:

$$CRRATEf = max \left[C_C - Need_C - \left(\frac{R_O}{AOCR} \right), 0 \right]$$

The total change of any non-particulate constituent j is calculated as:

$$\frac{\partial C_j}{\partial t} = \frac{N_{t+\Delta t} \cdot CRRATEf \cdot FC_jf + N_t \cdot M_{nat} \cdot WW_t \cdot DWWW \cdot FCDW_t \cdot FC_jfM}{\Delta V}$$

The distribution of recycled carbon to a model constituent (denoted as 'j'; e.g., RPOC, LPOC, etc.) by a living fish (FC$_j$f) is governed by fractions specified as input parameters to the model. Additional carbon recycling occurs due to natural mortality (M_{nat}); fishing mortality is lost from the system. The distribution of recycled carbon from mortality is controlled by fractions input to the model (FC$_j$fM).

Table 3
Constituent distribution of elements recycled from fish to the water column.

Constituent	FE$_j$F[a]	FE$_j$FM[b]
Carbon		
Dissolved organic carbon (DOC)	0.25	0.25
Labile particulate organic carbon (LPOC)	0.50	0.25
Refractory particulate organic carbon (RPOC)	0.25	0.25
Nitrogen		
Ammonium (NH$_4$)	0.56	0.55
Dissolved organic nitrogen (DON)	0.24	0.20
Labile particulate organic nitrogen (LPON)	0.10	0.20
Refractory particulate organic nitrogen (RPON)	0.10	0.05
Phosphorus		
Phosphate (PO$_4$)	0.50	0.50
Dissolved organic phosphorus (DOP)	0.40	0.40
Labile particulate organic phosphorus (LPOP)	0.05	0.07
Refractory particulate organic phosphorus (RPOP)	0.05	0.03
Silica		
Particulate silica (PS)	0.50	n/a
Dissolved silica (DS)	0.50	n/a

[a] FE$_j$F: Fraction of total mass of element E (e.g., C, N, P, or S) returned to the water column due to respiration, egestion, and excretion that is recycled to a particulate constituent.
[b] FE$_j$FM: Fraction of element E returned to the water column due to natural mortality that is recyled to a particular constituent.

For particulate matter, losses to fish consumption are also included:

$$\frac{\partial C_j}{\partial t} = \frac{N_{t+\Delta t} \cdot CRRATEf \cdot FC_jf + N_t \cdot M_{nat} \cdot WW_t \cdot DWWW \cdot FCDW_t \cdot FC_jfM - N_{t+\Delta t} \cdot V'_s \cdot [j]}{\Delta V}$$

In this equation, [j] is the concentration of constituent j (in g/m^3). Empirical data upon which to base the distribution of recycled carbon to the various model constituents were unavailable; therefore, the fractions employed by the water quality model for mesozooplankton were used for menhaden (Table 3).

The new fish carbon fraction is calculated from the actual consumption and recycling rates as:

$$FDCW_{t+\Delta t} = \frac{(WW_t \cdot DWWW \cdot FDCW_t + \Delta t \cdot (C_c - R_c - CRRATE_f))}{DWWW \cdot W_{t+\Delta t}}$$

For the nitrogen mass conservation is governed by:

$$G'_N = C'_N - (F'_N + U'_N)$$

Within the eutrophication model, algal/zooplankton nitrogen is accounted for as a fraction of each species' carbon concentration. Nitrogen uptake is governed by this fixed ratio and the nitrogen in the particulate matter consumed:

$$C'_N = V'_s \cdot \left[\sum_{k=1}^{3} (B_k \cdot Anc_k) + LZ \cdot ANClz + [LPON] + [RPON] \right]$$

Anc$_k$ is the algal nitrogen to carbon ratio (gN/gC); ANClz is the zooplankton nitrogen to carbon ratio (gN/gC) and LPON and RPON are labile and refractory particulate organic nitrogen. Following the calculations for carbon, the required nitrogen intake to maintain/achieve the target composition is calculated as:

$$Need_N = WW_{t+\Delta t} \cdot DWWW \cdot TFNDW - WW_t \cdot DWWW \cdot FNDW_t$$

Nitrogen recycling to the water column is therefore:

$$NRRATEf = F'_N + U'_N = C'_N - G'_N = max[C'_N - Need_N, 0]$$

And the rate of recycling of dissolved nitrogen becomes:

$$\frac{\partial N_j}{\partial t} = \frac{N_{t+\Delta t} \cdot NRRATEf \cdot FN_jf - N_t \cdot M_{nat} \cdot W_t \cdot DWWW \cdot FNDW_t \cdot FN_jfM}{\Delta V}$$

Whereas for particulate constituents (due to consumption as well as excretion by menhaden) the rate of change becomes:

$$\frac{\partial N_j}{\partial t} = \frac{N_{t+\Delta t} \cdot \text{NRRATEf} \cdot \text{FN}_j\text{f} + N_t \cdot M_{\text{nat}} \cdot \text{WW}_t \cdot \text{DWWW} \cdot \text{FNDW}_t \cdot \text{FN}_j\text{fM} - N_{t+\Delta t} \cdot V'_s \cdot [j]}{\Delta V}$$

The recycling fraction of nitrogen to each model constituent from egestion/excretion is based on empirical observation. In an omnivorous fish such as menhaden, the ratio of excreted nitrogen (U_N) to egested nitrogen (F_N) is approximately 80:20 (Baird et al., 2008), with 70% of the excreted nitrogen in the form of ammonia and 30% in the form of dissolved organic nitrogen (Durbin and Durbin, 1981). Egested nitrogen was assumed to consist of a 50/50 split between LPON and RPON, resulting in the FN_jf fractions given in Table 3. The new fish composition is calculated from consumption and recycling rates as:

$$\text{FNDW}_{t+\Delta t} = \frac{(W_t \cdot \text{DWWW} \cdot \text{FNDW}_t + \Delta t \cdot (C_N - R_c - \text{NRRATE}_f))}{\text{DWWW} \cdot W_{t+\Delta t}}$$

Calculations for phosphorus constituents are identical to those for nitrogen constituents. The ratio of excreted phosphorus (U_P) to egested phosphorus (F_P) is 90:10 (Baird et al., 2008). Egested phosphorus is assumed to consist of a 50/50 split between labile and refractory particulate organic phosphorus. Metabolized phosphorus is primarily excreted as phosphate in urine (Bureau, 2004), but the amount of phosphorus absorbed relative to growth is reliant on species and individual condition, therefore the distribution to phosphate and dissolved phosphorus was estimated as 50% and 40% of total recycled phosphorus (Table 3).

The fraction of fish silica is taken as zero; therefore all silica is recycled immediately to the two model constituents in a 50/50 split:

$$\frac{\partial \text{DS}}{\partial t} = \frac{\text{FDSf}}{\Delta V} \cdot N_{t+\Delta t} \cdot V'_s \cdot \left[\sum_{k=1}^{3} (\text{Asc}_k \cdot B_k) + \text{LZ} \cdot \text{ASClz} + [\text{PS}] \right]$$

$$\frac{\partial \text{PS}}{\partial t} = \left\{ \frac{\text{FDSf}}{\Delta V} \cdot N_{t+\Delta t} \cdot \left[\sum_{k=1}^{3} (\text{Asc}_k \cdot B_k) + \text{LZ} \cdot \text{ASClz} + [\text{PS}] \right] \right\} - N_{t+\Delta t} \cdot V'_s \cdot [\text{PS}]$$

[DS] and [PS] are the concentrations of dissolved and particulate silica. Rate of change of concentration of dissolved oxygen is related to the mass of oxygen consumed per fish, the population, and the cell volume:

$$\frac{\partial \text{DO}}{\partial t} = -N_{t+\Delta t} \cdot \frac{R'_o}{\Delta V}$$

Several assumptions and simplifications are inherent. Both mortality and the life processes are treated as instantaneous, with mass returning to the water column in the same time step as death/food consumption. Fish gastric evacuation rate and egestion/excretion composition are complex, nutrient-source dependent functions (Rippetoe, 1993) that must be simplified to fit within the confines of the model. Nutrient return from fish dying of natural mortality is also complex, particularly given the high predation level by other species, which process the menhaden before returning some portion of the mass to the water column (through their own life processes and mortality). The mass of menhaden consumed and recycled by predators is significant; striped bass alone were estimated to consume between 1.9 and 2.0 × 10⁸ kg of menhaden annually from 1994 to 1888 (Uphoff, Jr., 2003b), and the diets of age-2 and older striped bass, bluefish, and weakfish are estimated to consist of over 60% menhaden (Hartman, 2003).

Despite these limitations, nutrient recycling based on fish physiological data is included, allowing the model to capture feedback effects of the fish to the water column and retain conservation of mass. In addition, the estimates are conservative from the standpoint of top-down eutrophication modeling, in that all mass is returned to the model environment upon natural mortality, when in actuality some of the 'menhaden' nutrient mass incorporated into predators through growth would be removed from the system by migration and fishing mortality of the predator species.

2.7. Uncertainty analysis

An analysis was undertaken to determine how variability in the most uncertain model parameters would alter results. Amongst the bioenergetics parameters used, prior work (Megrey et al., 2007; Gottlieb, 1998b) has shown that fish growth is most sensitive to respiration parameters (RESA and RESB). Feeding fraction (F_{Frc}) also impacts consumption and growth; case studies were undertaken varying these parameters by ±5%. In addition, lack of fish physiological data introduces uncertainty in the recycling distribution of labile and refractory particulate nitrogen and phosphorus, so from the baseline case, assuming a 50/50 split of labile to refractory particulate matter, cases of 40/60 and 60/40 were considered for each nutrient. Finally, the uncertainty in distribution of phosphate and dissolved phosphorus through excretion was addressed by varying the excreted phosphorus from a 50/40 split of phosphate and dissolved phosphorus to a 60/30 and 40/50 split. Given that the primary interest of the current study is the impact of the fish on water quality, the model outputs considered were the average net primary productivity and algal biomass over the year and quantity of algal biomass during the spring bloom (taken on April 1). Also considered was the total fish biomass at that same instance.

3. Results

3.1. Menhaden growth

In order to validate the selection of appropriate bioenergetic parameters, calculated growth rate values can be compared to empirical observations. In Chesapeake Bay, the observed growth rate in age-0 menhaden sampled at the Chesapeake Biological Laboratory pier was between 1.2 and 6.6% of wet body weight per day (Rippetoe, 1993). Of the model predictions for age-0 fish, 30.8% fell within this range of values, with 64.5% of observations below 1.2% growth per day and 4.7% of observations above 6.6% growth per day (Fig. 3a), demonstrating that model growth is consistent with empirical observation.

Comparing model results to observed size of older fish implies a tendency toward under-prediction of growth in the age-1+ fish (Fig. 4), noting the relatively large standard deviation in observed values. Model fish growth over the season is reasonable compared to the lowest observed growth patterns in the field. The values of instantaneous growth rate for feeding model adult fish (Fig. 3b–d) are somewhat low compared with the available data on instantaneous daily growth rates for Atlantic menhaden (observed in Narragansett Bay) of ~1% for age-2 and age-3 fish (Durbin et al., 1983), again suggesting consumption and growth for older fish may be under-predicted. Given the lack of detailed data regarding growth throughout the season in Chesapeake Bay and that from a water quality standpoint an under-estimate of menhaden food consumption makes the predicted impacts more conservative, the model was not re-parameterized.

3.2. Consumption by menhaden

Specific instantaneous consumption rates exhibited a bimodal distribution as a result of parameterization into feeding and non-feeding states (Fig. 5), with consumption during feeding
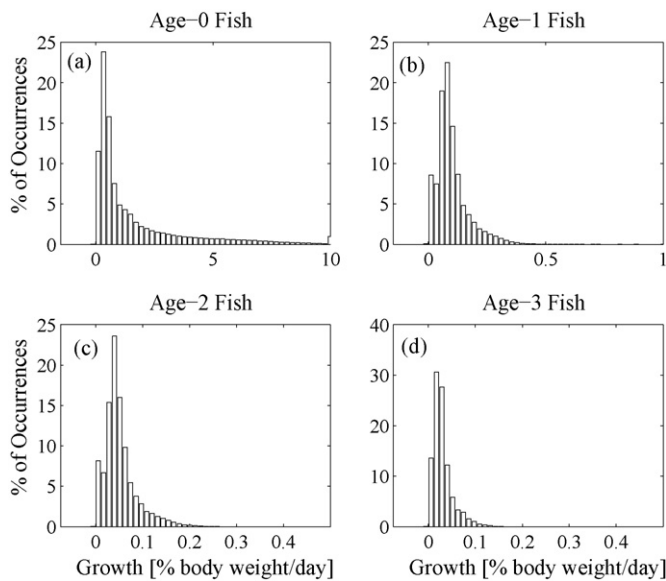
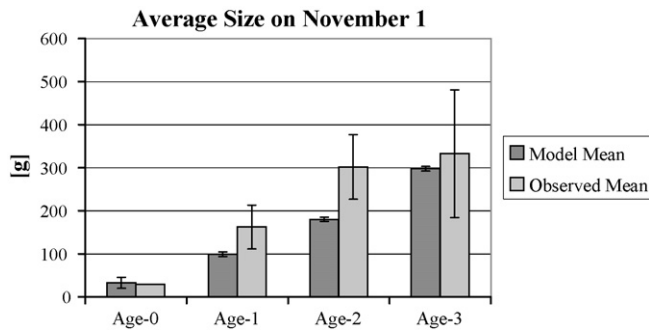**Fig. 3.** Modeled growth rate of menhaden for age-0 (a), age-1 (b), age-2 (c), and age-3 (d) classes.

Fig. 4. Observed and model menhaden size on November 1, with field data from Gottlieb (1998b).
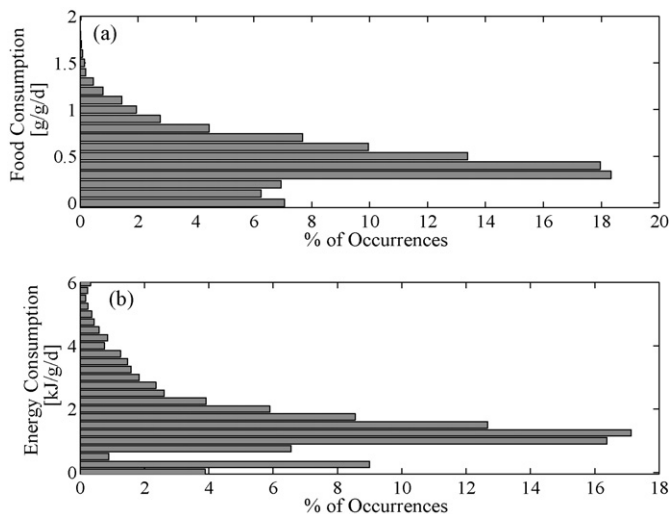

Fig. 5. Distribution of instantaneous consumption of food (a) and energy (b) on a consumption per gram of menhaden per day basis for age-0 fish.

Table 4
Mean energy consumption by menhaden (in kJ/g/d), sorted by age class and food type.

	Age-0	Age-1	Age-2	Age-3
Algae	1.2931	1.2215	1.1589	1.1263
Zooplankton	0.0315	0.0293	0.0279	0.0251
Detritus	0.2002	0.1893	0.1789	0.1779
Total	1.5248	1.4400	1.3657	1.3294

approximately 0.4 g/g/d or 1.3 kJ/g/d for age-0 fish. In laboratory experiments, consumption rates for age-0 menhaden (of *Artemia sp. nauplii*) were determined to range between 0.34 and 1.06 g/g/d or 0.91 and 2.79 kJ/g/d over a range of temperatures of 18.1–30.1 °C (Rippetoe, 1993), indicating that the model is estimating consumption within the range of observed values for age-0 fish. There was a slight decrease in the consumption rate on average with increasing age class (Table 4). Fish within the model have no food preference, filtering all prey with equal efficiency and at the same volumetric clearing rate, and the difference in energy consumption rates of phytoplankton, zooplankton, and detritus (Table 4) are a result of their relative concentration in the model environment and their energy density.

3.3. Haul by the fishery

The total weight of fish lost to fishing mortality was tracked for comparison with actual fishing hauls from Chesapeake Bay. The total east coast haul of Atlantic menhaden for 1955–2005 was between 150,000 and 700,000 metric tons per year, with average haul exhibiting an overall decline since 1955 (National Marine Fisheries, 2009). In recent years an estimated 52% of that haul was taken from Chesapeake Bay (Smith, 1999), for an estimated 78,000–364,000 metric tons of menhaden annually. In comparison, model fishing haul varies from 10,000 to 40,000 (in the twice baseline initial population case) metric tons. As previously mentioned, the mortality rates used are for the entire Atlantic stock, which is an underestimate of the fishing mortality rate for fish within Chesapeake Bay given the high concentration of fishing pressure there. In addition, the size-at-haul may be low using constant mortality throughout the year vs. a focused fishing effort during the fishing season when fish will be larger than they are at the beginning of the year. A more accurate measure could be attained by attempting to estimate a spatially variant Chesapeake Bay fishing mortality during the fishing season; however, insufficient observations presently exist for model calibration.

3.4. Effect on primary productivity and algal biomass

The primary interest of this study is the potential effect of menhaden on algae in Chesapeake Bay. The importance of including feedback to the water column can be observed by comparing the primary productivity in the zero population case to cases where fish are present (Table 5); overall, primary productivity increases in the presence of menhaden, mostly likely due to excreted nutrients in more readily accessible forms acting as fertilizer and increasing algal growth rates. In terms of algal biomass, however, the greater the fish population in the bay, the less algal biomass is present, indicating that menhaden are capable of 'keeping up' with the excess

Table 5
Average primary productivity and algal biomass for the year presented as a percent change from the baseline population case.

	No fish	Half baseline	Twice baseline	Five times baseline
Average primary productivity	−8.64%	−4.16%	7.17%	23.72%
Average algal biomass	0.86%	0.48%	−1.26%	−11.42%

Table 6
Analysis of variability in model outputs (as a percentage change from the baseline fish population case) with variation in the most uncertain model parameters.

	Fish biomass (April 1)	NPP (year average)	Algal biomass (year average)	Algal biomass (April 1)
Drop RESA by 5%	0.00%	−0.01%	−0.01%	0.00%
Raise RESA by 5%	−0.06%	−0.02%	−0.02%	0.00%
Drop RESB by 5%	0.00%	0.00%	0.00%	0.00%
Raise RESB by 5%	0.00%	0.00%	0.00%	0.00%
Drop F_{Frc} by 5%	−1.05%	−0.73%	0.08%	0.40%
Raise F_{Frc} by 5%	1.04%	0.74%	−0.09%	−0.40%
Particulate nitrogen LPON = 12%, RPON = 8%	0.00%	0.10%	0.02%	0.00%
Particulate Nitrogen LPON = 8%, RPON = 12%	0.00%	−0.10%	−0.02%	0.00%
Particulate phosphorus LPOP = 6%, RPOP = 4%	0.00%	0.00%	0.00%	0.00%
Particulate phosphorus LPOP = 4%, RPOP = 6%)	0.00%	0.00%	0.00%	0.00%
PO_4/dissolved phosphorus PO_4 = 60%, LDOP = 30%	0.00%	0.03%	0.00%	0.02%
PO_4/dissolved phosphorus PO_4 = 40%, LDOP = 50%	0.00%	−0.03%	0.00%	−0.02%
No fish	n/a	−8.64%	0.86%	6.42%
2× baseline population	97.55%	7.17%	−1.26%	−4.24%
5× baseline population	733.02%	23.72%	−11.42%	−26.28%

primary productivity caused by their presence, resulting in a net decrease in algal biomass.

These results can be expanded by considering the annual variation in primary productivity and algal biomass (Fig. 6a). Once again, the presence of menhaden generally results in an increase in primary productivity (Fig. 6b) as a result of nutrient recycling. During the spring bloom, when algal concentration is highest, menhaden decrease the overall biomass (Fig. 6c) as the fish consume highly concentrated food sources. In autumn, when menhaden commence their seasonal migration of the bay, there is an increase in algal biomass in the presence of fish compared to the no fish case. This effect is a result of an increase in primary productivity fueled by enhanced nutrient recycling in the wake of the schools, which have since departed and are no longer consuming algal biomass. The algal biomass begins to decrease as the recycled nutrients are depleted, however, and at its peak for the five times baseline case is only a 15% increase from the baseline population estimate as compared to a peak reduction in biomass of upwards of 30% in spring.

3.5. Uncertainty analysis

Varying the fish bioenergetics respiratory parameters, fish feeding fraction, and recycling distributions for particulate nitrogen,
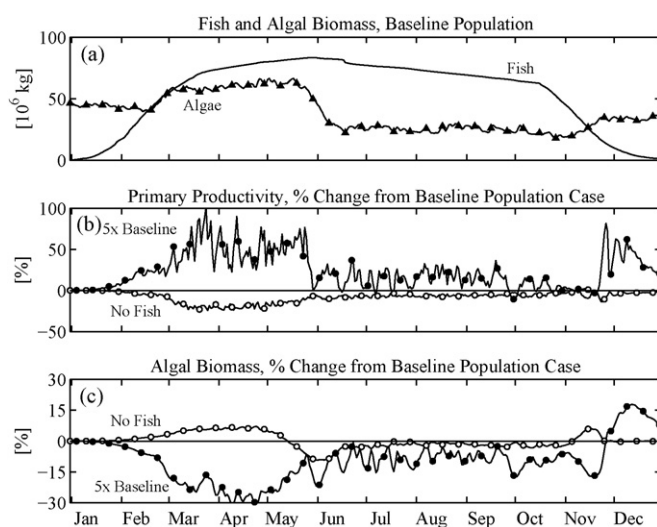

Fig. 6. Seasonal variation in algal and fish biomass for the baseline population case (a), along with primary productivity (b) and total algal biomass (c) as a percentage change from the baseline case for "historic" and zero population.

phosphorus, phosphate, and dissolved phosphorus produced negligible changes in the spring fish biomass. More relevant to the primary interest of menhaden impacts on water quality, the average net primary productivity and algal biomass over the year and the algal biomass during the spring bloom were also relatively insensitive to these parameters (Table 6). The percentage change from the baseline case was at or below 1%, significantly less than the change resulting from varying the initial fish population. Consequently, the uncertainty introduced from the fish parameterizations is less than that introduced by uncertainty in the fish population, and the water quality impacts observed with the changes in population considered in the current study are beyond what would be introduced by the uncertainty in model parameterization.

4. Discussion

When compared to field values, model consumption and growth rates are reasonable (although size predictions for older fish are on the low end of observed values), indicating the model is adequately modeling menhaden growth. In regards to impacts on the water column, the results indicate a complex relationship between fish and algae, including an increase in primary productivity in the presence of fish. This result indicates the percentage of a fixed value of primary productivity a population could consume may not be the most appropriate metric for determining the effect of predation by fish on algae, since fish nutrient recycling may increase the primary productivity. The increase in primary productivity does not result in an increase in algal biomass, which decreases with increasing fish population. This result is consistent with modeling efforts by Cerco and Noel (2004), who found an increase in generic algal predation may initially increase primary productivity as a result of enhanced nutrient recycling, while algal biomass decreases due to increased consumption, until a tipping point (not observed in the current study) is reached when algal stock is reduced significantly enough to again reduce primary productivity.

In addition to the role of nutrient recycling, this formulation captures menhaden as a seasonally and spatially variant consumer of seasonally and spatially variant prey. Although menhaden consume algae throughout the year, they are most effective when local algal concentrations around the school are high, allowing them to consume more biomass while filtering water at the same rate. The result is that their impact is comparatively larger when the algal biomass itself is high, and they have a dampening effect on algal biomass peaks; for example, during the spring bloom, which corresponds to the time of year when large numbers of menhaden may be found within the bay.

5. Conclusions

The purpose of the current study was to integrate a fish bioenergetics model into a spatially and temporally explicit eutrophication model, and to undertake a pilot study using the combined model to examine the impact of menhaden on water quality in Chesapeake Bay. Schools of fish have been added to the CE-QUAL-ICM framework, with spatial distributions calibrated to be consistent to those observed in the field. Model constituents decrease as a result of consumption, itself a function of physiological fish parameters and food availability, and a bioenergetics module converts consumed energy and food into growth and determines the rates at which non-sequestered nutrients return to the water column.

The model was applied to Atlantic menhaden, a planktivorous fish found in Chesapeake Bay. Menhaden are found to have a disproportionately large effect when algal concentrations are highest, demonstrating that a spatially explicit and temporally explicit model of fish and their consumption is necessary to capture their impacts on spatially variant and temporally variant prey sources (particularly those with nonlinear biomass growth curves) such as phytoplankton. In addition, the presence of menhaden has been determined to potentially increase primary productivity while still decreasing net algal biomass, underlying the importance of considering nutrient recycling by these fish. Future improvements to the model may include the addition of fish behaviors to describe movement and thus refine their distribution pattern; incorporation of additional higher trophic level organisms, which devour primary consumers such as menhaden; and the treatment of algae as discrete particles to model highly concentrated patches which may increase the efficiency of model fish consumption.

Acknowledgements

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